

THE MECHANICS OF FISH SKIN: LACK OF AN "EXTERNAL TENDON" ROLE IN TWO TELEOSTS

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ABSTRACT

The skin of the Norfolk spot, *Leiostomus xanthurus*, is composed largely of a crossed-helical array of collagen fibers. Over most of the body of the fish these are oriented at angles of 45–80° with the long axis of the fish. The skin of the skipjack tuna, *Katsuwonus pelamis*, also contains a crossed-helical array of collagen fibers, although fewer fiber layers are present and fiber angles are generally in the range of 55–75°. Uniaxial stress-strain tests indicate that for both species skin is most extensible in the longitudinal direction. For the Norfolk spot, skin is stiffer in the direction of the fibers than in the circumferential direction, but for the skipjack tuna, the skin is of about the same stiffness in the circumferential direction as it is in the direction of the fibers. Biaxial stressing tests demonstrate that the skins of the spot and the skipjack do not behave as simple crossed-fiber systems, and are therefore incapable of transmitting forces down the lengths of these fishes or acting as "external" tendons.

INTRODUCTION

The skin of fishes is composed largely of a system of collagen fibers that form alternating layers of right and left helices wrapped about the long axis of the animal. This arrangement of collagen fibers simultaneously provides a supporting framework to enclose the body contents and a flexible covering to allow whatever changes in shape are necessary during locomotion. This crossed-fiber arrangement has been described in elasmobranchs (Motta, 1977; Wainwright *et al.*, 1978) and teleosts (Fujii, 1968; Nadol *et al.*, 1969; Brown and Wellings, 1970; Hawkes, 1974; Willemse, 1972; Videler, 1975; and Hebrank, 1980).

Engineers use this design feature for reinforcing thin-walled pressurized cylinders by winding them with inextensible fibers. With this design a lightweight cylinder wall is created that can strongly resist internal pressures, yet is capable of extensions in any direction except those of the fibers themselves. In the directions of the circumference and long axis of the cylinder, large extensions are permitted (these are the directions that bisect the angles between a pair of crossed-helices) and because the fibers are inextensible, torsion of the cylinder is also strongly resisted. The angle that the helices make with the long axis of the cylinder is called the fiber angle, and for a range of fiber angles excluding those near 0° and 90°, the cylinder can be bent without kinking or wrinkling. The convex side of a bent constant volume cylinder is stretched in the longitudinal direction; on this side the fiber angle decreases. The reverse occurs on the opposite or concave side. In this way the cylinder (or a fish) can undergo a range

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of movements without changing its body form or volume (Clark, 1964) and without kinking or wrinkling, which is important to hydrodynamic stability.

The importance of a crossed-fibrillar array of collagen to fish locomotion was first demonstrated by Wainwright *et al.* (1978) with their study of shark skin. These authors found the skin to be capable of acting as an external tendon, transmitting force and displacement in parallel with the attached, underlying muscles. Because a force applied to the skin can generate a greater bending moment than the same force applied near the backbone, the mechanical advantage of the axial musculature can be enhanced by pulling on skin that is capable of transmitting forces down the length of the fish. A subsequent study by Hebrank (1980) concluded that the skin of the American eel (*Anguilla rostrata*) is also capable of serving as an external tendon.

Sharks and eels, however, are considered to be relatively primitive fishes, and both swim using fairly large amplitude waves of lateral undulation. In this study the structural features and mechanical properties of the integuments of two more advanced teleosts, the Norfolk spot (*Leiostomus xanthurus*) and the skipjack tuna (*Katsuwonus pelamis*), were studied in a manner similar to those used to investigate the mechanics of shark and eel skin. Neither of these fishes exhibits the degree of lateral undulation in swimming characteristic of eels and sharks, therefore the purpose of this study was to determine whether the skins of these two teleosts are capable of serving as external tendons.

MATERIALS AND METHODS

Experimental animals

Five Norfolk spots (*Leiostomus xanthurus*) ranging in standard length from 16 to 21 cm, and 4 skipjack tunas (*Katsuwonus pelamis*) whose fork lengths ranged from 44 to 50 cm were used for the mechanical tests and histological studies described below. The spots were obtained fresh from a local seafood market and the skin was either removed and studied at once or else the entire fish was frozen until its skin was needed. The tunas were obtained from the National Marine Fisheries Service Laboratory at Kewalo Basin, Honolulu, Hawaii; and transported frozen to North Carolina where the skin was removed from the frozen carcasses for testing.

Structure of the skin

For both species cryostat (American Optical, Model 830) sections 10 microns thick were made from fresh skin samples, mounted on slides with distilled water, and examined using a Leitz Ortholux polarized light microscope.

Mechanical testing

Uniaxial tensile stress tests were performed on skin samples in order to quantify stress-strain relationships in the direction of the collagen fibers and in both the longitudinal and hoop (circumferential) directions on the fish. Square or rectangular skin samples measuring several centimeters on a side were cut from the fish between the dorsal and ventral midlines and between the pectoral fins and the caudal peduncle. As much muscle was removed from the skin as possible using razor blades and scissors. Snap-swivels or alligator clips connected to fishing leader wire were attached to the edges of the samples for testing in the stress-strain machine described elsewhere (Wainwright *et al.*, 1978). To test for extension in the fibers themselves, skin samples were cut and stressed parallel to the previously determined fiber angle; during stressing, the

orthogonal sides of the skin were allowed to deform freely. In a similar manner skin was cut and stressed uniaxially in the hoop and longitudinal directions.

An additional series of stress-strain tests was conducted by applying an increasing tensile load to the longitudinal axis while maintaining the hoop axis at a constant stress, and while monitoring strains of both the longitudinal and hoop axes simultaneously. The constant hoop stress applied in these tests was 0.12 MN/m^2 , a value chosen to correspond with the more extensible lower range of the longitudinal stress-strain curves, and therefore a value likely to fall within the *in vivo* range of stresses occurring during normal swimming movements. The purpose of these biaxial stressing tests was to determine the relative contributions of the crossed-fiber system and the interfibrillar matrix material to the mechanical properties of the whole skin. If the extensibility of the skin is controlled solely by the helical fibers, the ratio of the hoop to longitudinal stresses applied is always equal to the tangent of the fiber angle resulting from these stresses times the tangent of the initial fiber angle. Using this relationship a longitudinal stress-strain curve can be constructed for any constant hoop stress applied, which will predict skin properties if they are due only to a set of continuous fibers. Comparison with the experimentally obtained stress-strain curve for whole skin should allow the roles of the fibers and the matrix to be assessed.

RESULTS

Structure of the skin

The skin of the Norfolk spot is typical of most teleosts, consisting of a covering of ctenoid scales that are anchored to the pigmented epidermis and are surrounded by a clear gelatinous material. Beneath the epidermis is the stratum compactum, or the collagenous layer of the skin. Microscopy reveals that alternating sheets of parallel fibers comprise this layer. Figure 1 is a polarized light micrograph of a section cut

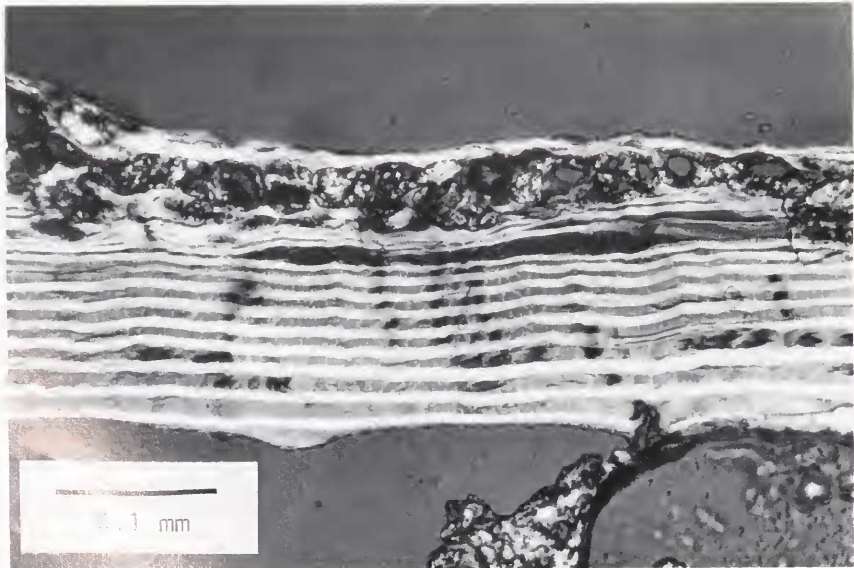


FIGURE 1. Polarized light micrograph of a radial section of spot skin cut parallel to one set of fibers; 12 fibers (or fiber layers) can be seen in long section.

perpendicular to the skin and parallel to one set of fibers; twelve fibers (one per layer) can be seen in long section. The fibers are generally smaller in diameter in the outermost layers of the skin, and range in thickness from about 4 to 10 μm . The total skin thickness for animals of this size class (about 20 cm standard length) examined ranged from about 220 to 300 μm .

Fiber angles were determined at numerous locations on the fish and those obtained from one specimen are shown in Figure 2. In general the angles of the forward leaning fibers were lower than those of the corresponding backward leaning fibers, with the former ranging from 45 to 62° and the latter from 62 to 80°. The fibers of the dorsal half of the caudal peduncle, however, were exceptional, with the forward leaning fibers forming an angle of 75° with the long axis of the fish and the backward leaning fibers forming an angle of only 30°. In all cases, the fiber angles of the forward leaning fibers were examined within a few degrees of the pitch of the scale rows that overlay the collagenous layer of the skin.

The skin of the skipjack tuna, like other tunas, differs from the skin of most teleosts in that it is devoid of scales over most of its surface. Scales are present only in an irregularly shaped region just behind the opercular opening; this scaled region is known as the "corselet." A thin layer of pigmented epidermis covers the rest of the fish, and this is easily abraided to reveal the fine collagen fibers below. The stratum compactum is only a thin, nearly transparent layer in this fish, and once the pigmented epidermis is abraided the axial musculature is readily visible through the collagenous layer.

Microscopy reveals that alternating sheets of parallel fibers comprise this layer, just as they do in the spot. Figure 3 is a polarized light micrograph of a section cut perpendicular to the skin and parallel to one set of fibers. Three fibers (one per layer) can be seen in long section and between these, fibers of the alternating three layers can be seen in oblique end section. The fibers near the upper and lower boundaries of the skin are the thinnest, about 20 μm in diameter, while those occupying the center of the skin's thickness are much thicker, about 80 μm in diameter. The total skin thickness for skipjack tunas of this size class (about 45 cm fork length) ranged from about 280 to 350 μm .

Fiber angles varied widely with respect to position on the fish, and like the spot, were generally not the same in the forward and backward leaning directions at the same point on the fish, as shown in Figure 4. In the middle regions of the fish fiber

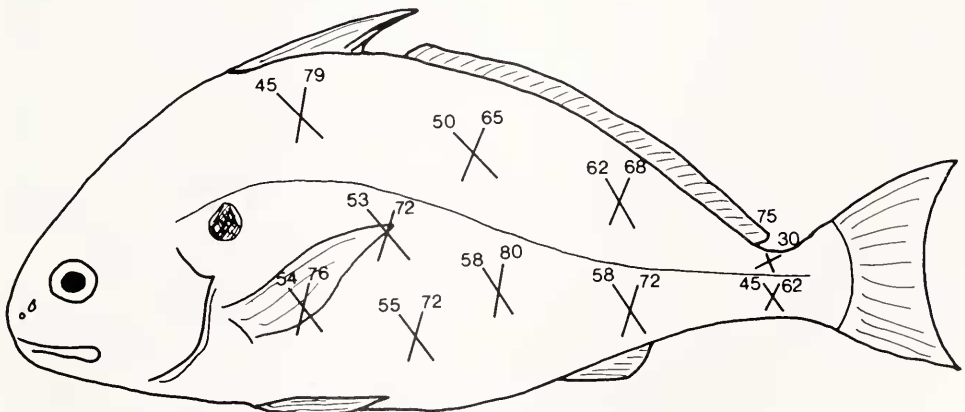


FIGURE 2. Fiber angles (in degrees) measured at various locations on one Norfolk spot specimen.

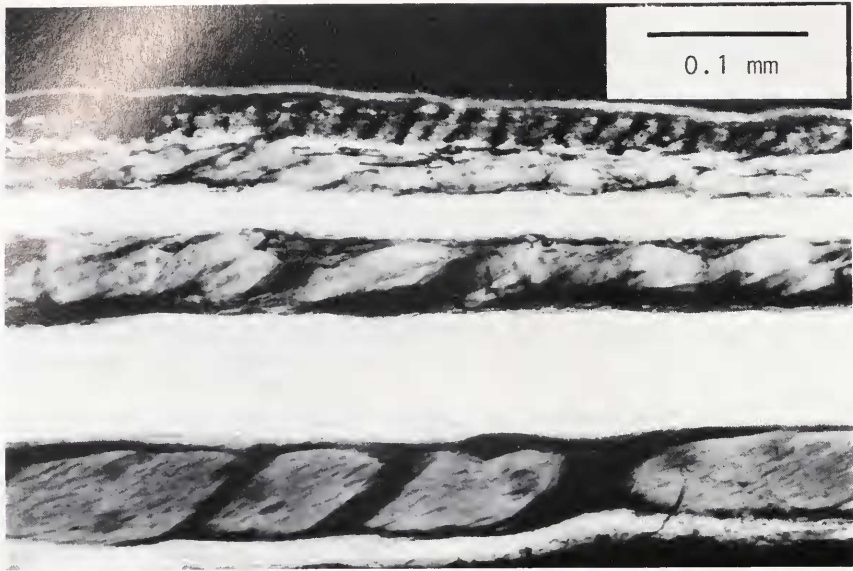


FIGURE 3. Polarized light micrograph of a radial section of skipjack tuna skin cut parallel to one set of fibers. Three fibers (or fiber layers) can be seen in long section alternating with three layers of fibers shown in oblique end section.

angles generally fell between 55 and 75° , but near the mid-dorsal and mid-ventral lines fiber angles became as low as 20° and as high as 87° . Fiber angles could be seen to change by several degrees as the mid-dorsal and mid-ventral lines were traversed and also changed slightly as the lateral line was traversed. In some cases fibers could be seen to curve as they suddenly changed pitch near the dorsal and ventral midlines.

Mechanical testing

In Figures 5 and 6 the results of uniaxial tensile tests are shown in the form of stress-strain curves for skin stretched in the direction of one set of fibers and in the hoop and longitudinal directions for each of the two species. For the skin of the Norfolk spot stretched in the direction of the fibers very low extensions are obtained

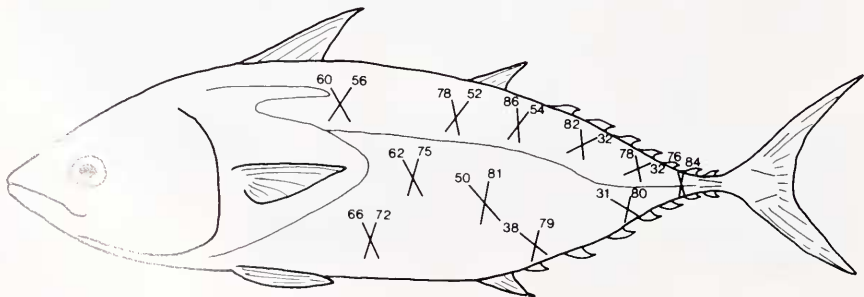


FIGURE 4. Fiber angles (in degrees) measured at several locations on one skipjack tuna specimen.

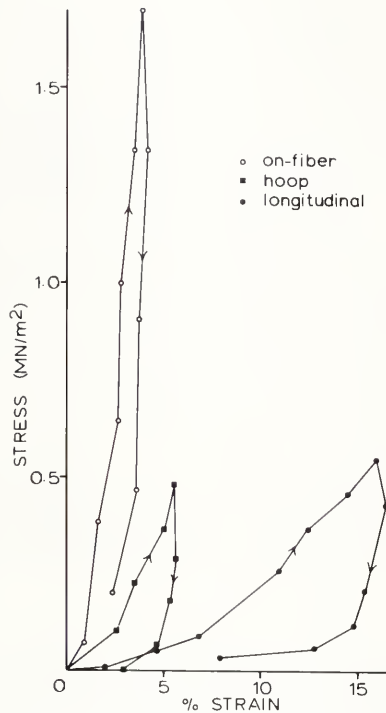


FIGURE 5. Typical stress-strain curves obtained for spot skin stretched uniaxially in the on-fiber, hoop, and longitudinal directions.

at high stresses. The fibers therefore appear to be reasonably inextensible, especially within the range of stresses applied to the hoop and longitudinal directions. The elastic modulus (the slope of the stress-strain curve in its steep region) obtained as an average of fifteen on-fiber pulls is 75.0 MN/m^2 , as shown in Table I.

The stress-strain curves for skin of the spot subjected to uniaxial stretching in the hoop and longitudinal directions reveal anisotropy in the mechanical properties of the skin. Skin stressed in the hoop direction exhibits a J-shaped curve in which the skin extends by several percent while the stress remains low, then following this initial extension the stress-strain curve becomes steeper as the skin deforms less freely under the applied load. In contrast, skin stressed in the longitudinal direction exhibits a more linear stress-strain curve as it extends fairly uniformly over the range of stresses applied. The mean terminal elastic modulus for spot skin pulled in the longitudinal direction is 2.4 MN/m^2 , which is significantly lower ($F_{(1,23)} = 14.4$, $P < 0.001$) than that of skin pulled in the hoop direction, a value of 16.4 MN/m^2 . In addition, the skin is significantly stiffer in the on-fiber direction than in the hoop direction ($F_{(1,25)} = 13.9$, $P < 0.001$).

Like the skin of the spot, that of the skipjack tuna is relatively inextensible in the direction of the fibers, as shown in Figure 6. However, in contrast to the spot, skin of the tuna stressed in the hoop direction is about as stiff as skin stressed in the on-fiber direction. The mean elastic modulus of the skin stressed in the hoop direction is 60.2 MN/m^2 , while that of skin stressed in the on-fiber direction is 36.2 MN/m^2 , as shown in Table I, although these differences are not significant ($F_{(1,29)} = 1.96$, $P = 0.20$).

The skin of the tuna stressed uniaxially in the longitudinal direction is similar to

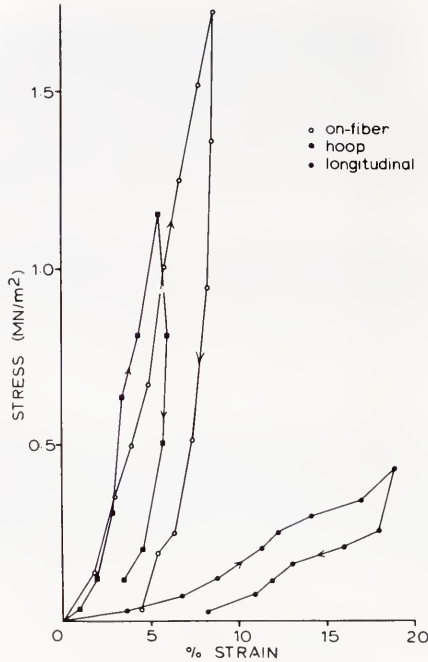


FIGURE 6. Typical stress-strain curves obtained for skipjack tuna skin stretched uniaxially in the on-fiber, hoop, and longitudinal directions.

that of the spot in that its stress-strain curve is more linear in shape and the skin is quite extensible. The differences in stiffness for skin stressed in the longitudinal direction compared to skin stressed in both the hoop and on-fiber directions are significant: for longitudinal *versus* hoop, $F_{(1,36)} = 17.16$, $P < 0.001$, and for longitudinal *versus* on-fiber, $F_{(1,29)} = 27.51$, $P < 0.001$. The mean elastic modulus for skipjack tuna skin stressed in the longitudinal direction is 6.9 MN/m^2 , an order of magnitude lower than those of the other two directions tested.

TABLE I

Comparison of mean terminal elastic moduli for skin of the Norfolk spot and the skipjack tuna stressed uniaxially in three directions

	Norfolk spot elastic modulus	Skipjack tuna elastic modulus
On-fiber	$7.50 \times 10^7 \text{ N/m}^2$ (S.D. = 4.99×10^7) (n = 15)	$3.62 \times 10^7 \text{ N/m}^2$ (S.D. = 2.30×10^7) (n = 12)
Hoop	$1.64 \times 10^7 \text{ N/m}^2$ (S.D. = 0.63×10^7) (n = 12)	$6.02 \times 10^7 \text{ N/m}^2$ (S.D. = 5.44×10^7) (n = 19)
Longitudinal	$2.41 \times 10^6 \text{ N/m}^2$ (S.D. = 2.26×10^6) (n = 13)	$6.92 \times 10^6 \text{ N/m}^2$ (S.D. = 4.25×10^6) (n = 19)

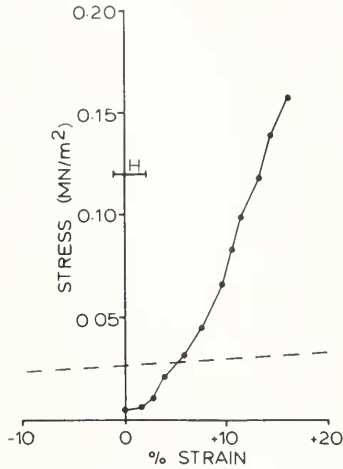


FIGURE 7. Biaxial stress-strain curve obtained for spot skin pulled in the longitudinal direction while the hoop direction was held at a constant stress of 0.12 MN/m^2 . A theoretical curve for a pure fiber model subjected to the same ratio of stresses is shown as a dashed line. The bar labeled H shows the range of strains recorded in the hoop direction.

Breaking stresses and strains could not be determined for skin from either fish pulled in any direction. On application of high loads (approximately 50% higher than those shown in Figures 5 and 6 for each skin direction) the skin always failed at the clips attaching the skin to the testing device.

In general, skin samples pulled in each of the three directions did not return to

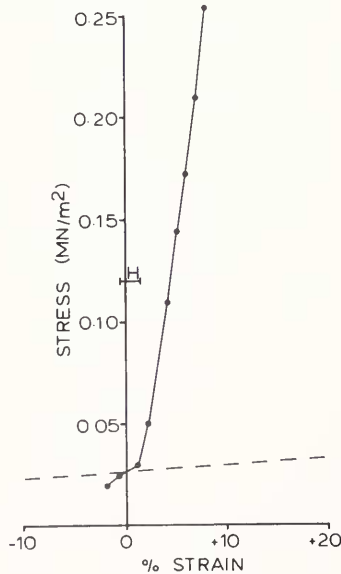


FIGURE 8. Biaxial stress-strain curve obtained for skipjack tuna skin subjected to the same conditions as in Figure 7.

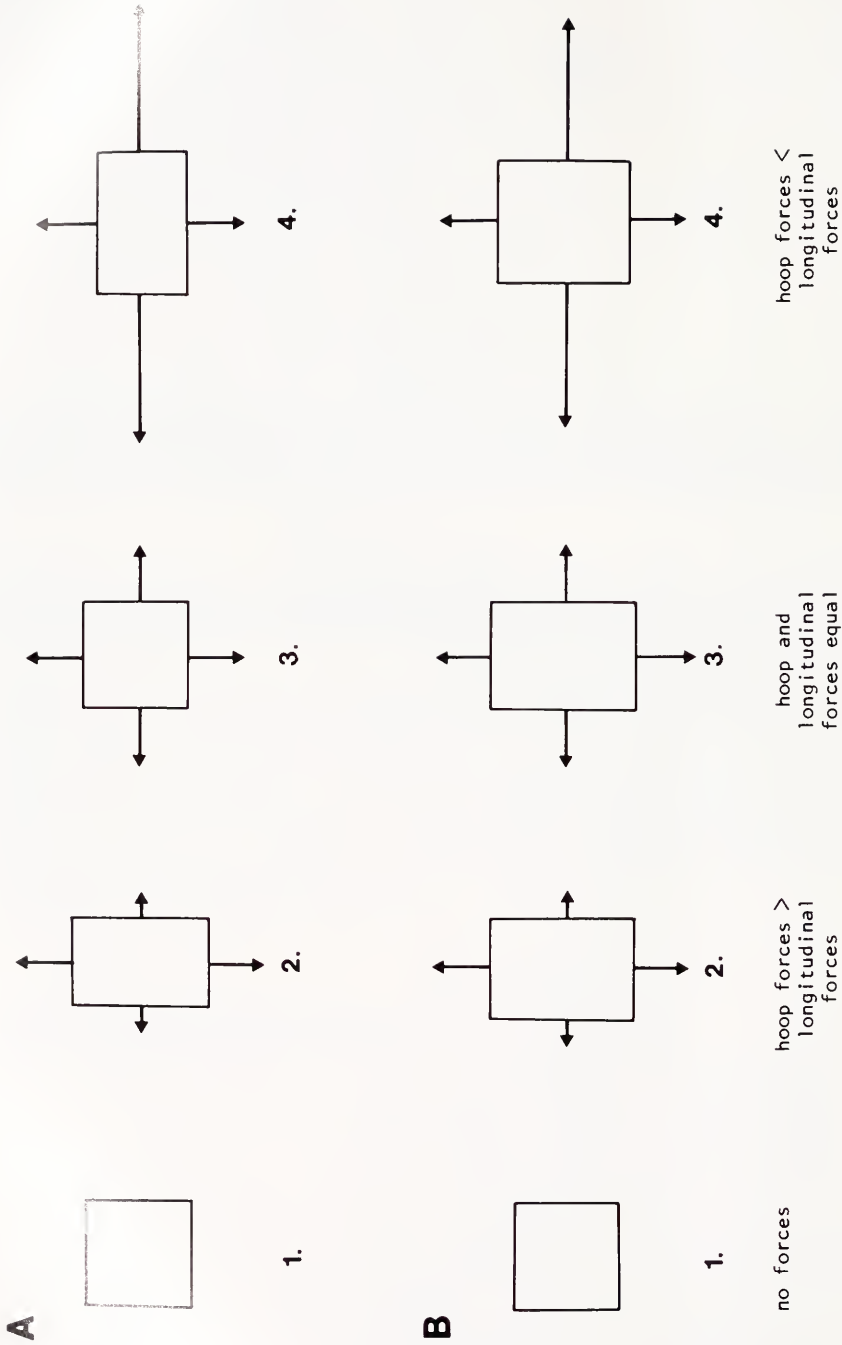


FIGURE 9. Schematic diagram of the behavior of (a) a simple crossed-fiber system, and (b) the skins of the spot and the tuna in biaxial stressing tests. The lengths of the arrows indicate the relative magnitudes of the forces applied to the hoop and longitudinal axes.

their original lengths once the load was removed, and the unloading curves always fell below the corresponding loading curves. However, this hysteresis may be exaggerated by frictional losses inherent in the testing device.

Biaxial stressing tests demonstrate that the skins of the spot and the skipjack do not behave as simple crossed-fiber systems. Stress-strain curves for tests performed in which the hoop axes were maintained at a constant stress of 0.12 MN/m^2 are shown for both fishes in Figures 7 and 8. Also shown in these figures are graphs of the predicted curve, based on the continuous fiber model described previously, subjected to the same ratio of stresses applied to the skin and having an initial fiber angle of 65° . It can be seen from these graphs that the skin of neither the spot nor the skipjack behaves in a manner similar to the model. Both are considerably stiffer than the model, having steeper curves than predicted, yet both require lower stresses applied to the longitudinal axes to achieve large initial extensions prior to crossing the predicted curve.

It is important to note that negative strains obtained for both the hoop and longitudinal directions were very small. Under these biaxial conditions much larger negative strains should have been observed, since the crossed-fiber system should allow both shrinking and stretching to occur simultaneously in the orthogonal sides of the skin. Instead, for both the spot and the skipjack, it appears that other material components within the skin dominate over the crossed-fiber system, as shown diagrammatically in Figure 9.

In this figure, row A depicts the behavior of a crossed-fiber model and row B depicts that of spot and tuna skin. When hoop forces are applied that exceed the longitudinal forces, the skin shown in B2 extends in the hoop direction but fails to contract in the longitudinal direction. In contrast, the model shown in A2 does contract in the longitudinal direction, and it therefore maintains a constant area. When longitudinal forces that equal the still-present hoop forces are applied to the model (A3), it extends in the longitudinal direction while contracting in the hoop direction. (Because forces are equal in both directions, it now has the same dimensions as it had in A1, before any forces were applied.) The skin shown in B3, however, does not contract in the hoop direction and extends very little in the longitudinal direction. (Its area has increased.) Much greater longitudinal forces are required (B4) to obtain both hoop contraction and longitudinal extension in the skin. The same longitudinal forces applied to the model (A4) result in greater degrees of both hoop contraction and longitudinal extension, with no increase in area.

DISCUSSION

The collagenous layers within the skin of both the Norfolk spot and the skipjack tuna occupy the major part of the skin's thickness, and this relatively thick collagenous layer accounts for the skin's strong construction. In this respect the skins of these fishes are similar to those of both the eel and the shark, however, relative to total body size the spot and the tuna both have skin that is comparatively thin.

Mechanical tests of the skins of these fishes reveal other similarities and differences: while the terminal elastic moduli are similar in cases of uniaxial stressing in the hoop and longitudinal directions, the skin of the spot and skipjack both become stiffer at lower extensions than does eel skin. In the directions of the fibers themselves the skin is an order of magnitude less stiff than that of the eel, indicating that either the fibers themselves are not continuous over the lengths of the skin samples tested, or else the fine fibrils that comprise the fibers pull apart from each other when loaded directly along their axes.

More important, however, the skin of the spot and the skin of the skipjack do not undergo the shape changes expected of a crossed-fiber system, thus the skin is not capable of transmitting forces down the length of the fish. In a fish such as the eel or the shark, muscle contraction in the anterior region bends the fish, and so the skin on the outer side is extended in the longitudinal direction. This extension, however, produces contraction in the hoop direction as the fiber angle decreases, until these dimensional changes are resisted by pressurization of the body fluids beneath the skin. Now the skin becomes stiff, and further longitudinal force applied to the skin by the anterior muscles results in tension transmitted to the tail by the skin. In this way the skin of the eel or the shark can act as an external tendon, as suggested by Wainwright *et al.* (1978).

The results of biaxial tests of spot and skipjack skin reported here demonstrate that contraction of one side of the skin does not occur concomitant with extension of the orthogonal direction. Without this contraction tension cannot be transmitted by the skin down the length of the fish during swimming movements. Although the skin appears to have helically arrayed fibers suitable for an external tendon, it cannot function as one. Instead, for the spot and the skipjack, the crossed-fiber array of collagen seems to function primarily to keep the tough exterior surface of the fish smooth and free of kinks during swimming movements. A smooth surface is an important factor promoting hydrodynamic performance.

It is interesting to note that while eels and sharks possess skin capable of acting as an external tendon, this study suggests that teleosts in general probably do not. Eels and sharks share one feature of the skin that may relate to the ability to transmit forces: they have extremely thick skin. A thick skin is clearly beneficial to these fishes in consideration of some of their peculiar behaviors; some sharks have been observed to bite each other during courtship and eels spend much of their time burrowed beneath the substrate. In contrast, most teleosts have skin that is much thinner in proportion to their body size and with a reduction in skin thickness apparently comes a loss in the ability to transmit forces. Webb and Skadsen (1979) recently suggested that a reduction in skin mass is related to a fish's ability to accelerate rapidly during prey capture, and so it seems likely that those fishes that rely on this "stalk and sprint" method of feeding have skins with mechanical properties similar to the Norfolk spot and the skipjack tuna.

There is another morphological feature common to the eel and the shark but not to most advanced teleosts, and this is the arrangement of the axial musculature. Alexander (1969) described two patterns of the axial musculature of fishes, which he termed the "selachian" and "teleost" arrangements. Relevant to this study is the fact that the selachian pattern is found in the sharks, eels, *Amia*, *Acipenser*, and *Salmo*, while the teleost pattern is found in virtually all other teleosts that swim using lateral undulations of the body. In addition, Willemse (1972) noted that in the eel and the shark the myosepta are thickened at the periphery of the fish where they attach to the skin; such thickenings are not found in the spot or the tuna. Finally, those fishes having the selachian arrangement of the axial musculature tend to have relatively high vertebral numbers: eels and sharks have over 100 vertebrae, *Amia* has about 80, *Acipenser* has about 100, and *Salmo* has about 60. In contrast, tunas in general have about 35-40 vertebrae and the spot has only 24.

These similarities and differences suggest that perhaps those fishes in which the selachian muscle arrangement and high vertebral numbers are found also have skin capable of acting as an external tendon, although the functional relationships between these three components are unknown. In his functional analyses of the selachian and teleost muscle arrangements Alexander (1969) concludes that the selachian arrange-

ment allows for the development of greater bending forces than does the teleost, but the teleost arrangement allows the fish to bend more quickly than the selachian. It is also important to recognize that anguilliform swimmers (eels and sharks) must transmit forces over a longer portion of the propulsive wave compared to the subcarangiform swimmers (e.g., the spot) and the thunniform swimmers (tunas). It may prove possible, then, that fishes utilize one of two methods of swimming: contractions of the axial musculature, which bend the fish more slowly, do so in such a way as to generate forceful bending moments and the forces generated may be transmitted by the skin; or by contractions of the axial musculature that bend the fish more rapidly at the expense of weaker bending moments, and the forces developed by the muscles cannot be transmitted by the skin. Examination of the skins of *Amia*, *Acipenser*, and *Salmo*, as well as additional advanced teleosts, are needed before such positive correlations between muscle, skin, and backbone types can be established.

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